# THE LATE TRIASSIC REPTILE *TERATOSAURUS*—A RAUISUCHIAN, NOT A DINOSAUR

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ABSTRACT. *Teratosaurus*, based on a maxilla from the late Triassic of Germany, is shown to have been a rauisuchian, and not a dinosaur. The Family Teratosauridae, based on skull remains and skeletons from around the world, is not an early radiation of carnivorous dinosaurs: it consists of the skeletons of prosauropod dinosaurs and the skulls and teeth of rauisuchians, or unidentifiable archosaurs. Other records of middle Triassic dinosaurs are also suspect. The Rauisuchia was a widespread and important group of large carnivores in the middle and late Triassic, and they had no close relationship with any dinosaurs.

ACCORDING to most current classifications of the dinosaurs, there was an extensive group of large carnivorous forms present in the middle and late Triassic (240–208 Ma), variously named Teratosauridae, Palaeosauridae, Zanclodontidae, or Gryponychidae (Romer 1956; Colbert 1964; Charig *et al.* 1965; Olshevsky 1978; Lambert 1983). Colbert (1970) elevated this assemblage to the Infraorder Teratosauria. This group has been viewed as an early major radiation of carnivorous dinosaurs that did not bear a close relationship to the typical Jurassic and Cretaceous carnosaurs. The genus *Teratosaurus* was established in 1861 (Meyer 1861) on the basis of a maxilla bearing large dagger-like teeth. Subsequently, further isolated carnivorous teeth and partial jaws, as well as large amounts of postcranial material, were associated with this genus. I show here that the type jaw of *Teratosaurus* belongs to a rauisuchian, a group of thecodontians that were distributed world-wide in the middle and late Triassic. The skeletons belong to a different group—the prosauropod dinosaurs (Walker 1964; Charig *et al.* 1965).

### *Teratosaurus suevicus* Meyer, 1861

*Type specimen.* British Museum (Natural History), BMNH 38646

*First description.* Meyer 1861: 258–271, pl. 45.

*Locality.* Heslach, near Stuttgart (Ströbel and Wurm 1977) 'on the other side of the valley' from the site of an earlier dinosaur find (Meyer 1861). Possibly the old quarry centred at $^{35}105^{54}007$ (map sheet 7220), labelled 'Stbr.' (Steinbruch, quarry); now filled and used as a Sportplatz.

*Age.* Mittlerer Stubensandstein, Mittelkeuper, Middle Norian, Upper Triassic (Brenner 1973).

The specimen (text-fig. 1) is a right maxilla (Walker 1964), not a left one, as was originally assumed (Meyer 1861; Huene 1908). The specimen measures 235 mm long (or 245 mm with a small additional piece at the front). In lateral view (text-fig. 1*a*), the remains of six teeth (2–7) may be seen. A detached flake of bone (not shown here) fits over the first two teeth, and it contains a third small tooth (1) in front of them. In medial view (text-fig. 1*b*), five teeth are seen below the edge of the jaw. At the front of the maxilla is a ledge which covers a deep socket (ps) for reception of the premaxilla. There are various pits (v?) on the inside of the maxilla which may be blood vessel and/or nerve openings. The most interesting area is the tooth-bearing portion. On the inside of the maxilla (text-fig. 1*b*) can be seen an apron or pedestal that overlies the teeth. There is a line of holes (rp), one for each tooth, and the bone below is characterized by small pits, 1 mm in diameter. The

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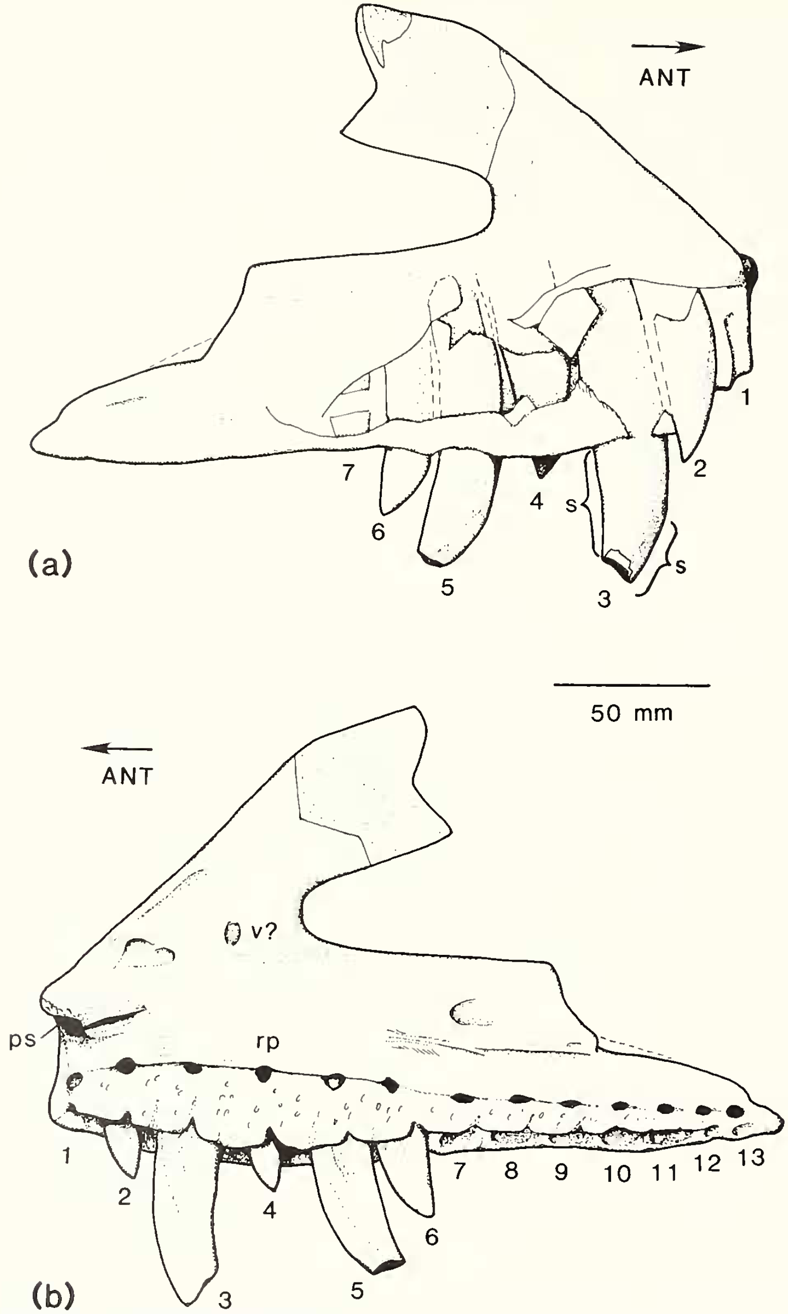


TEXT-FIG. 1. *Teratosaurus suevicus*, type specimen, BMNH 38646. Left maxilla. *a*, lateral view; *b*, medial view. The surface of the bone is much cracked and it has been repaired with glue, and coated with thick varnish in places. The upper portion (stippled) is partly unprepared—it consists of whitish-grey sandstone and glue. The teeth and tooth-sockets are numbered 1–13 from the front. ANT, anterior; ps, socket for the premaxilla; rp, tooth replacement pit; s, the serrated zones of the anterior and posterior tooth edges; v?, blood vessel or nerve opening (?).

lateral edge of the maxilla comes lower than this medial ledge, and it is visible in medial view. The holes are replacement pits through which new tooth buds passed from the medially lying dental lamina to become fixed in the bone of the jaw. The pitted bone appears to be highly vascular and was probably constantly remodelled as new teeth passed through it, and the teeth grew into occlusion. The lower edge of the medial apron is scalloped at the midline of each tooth.

Seven teeth are preserved in one form or another in this specimen in the anterior sockets (1–7). The posterior six sockets (8–13) have no teeth in them. There appcars to be some sort of variation in tooth size: 1, 2, 4, and 7 are small and barely erupted, 6 is a little larger, and 3 and 5 are the largest. The roots of full-sized teeth are very long, 50–60 mm for a crown length of 40–50 mm. In cross-section the teeth are oval and laterally compressed at the level of the jaw margin, and their long axes run from anteromedial to posterolateral. Just below the jaw edge the posterior margin of the tooth becomes pinched into a sharp knife-like edge with 3 serrations per mm. The front edge of the tooth remains rounded down to a slight ‘shoulder’ half-way down the crown (text-fig. 1*a*, s), where this edge also becomes sharp and serrated.

## DISCUSSION

### *Teratosaurus a rauisuchid*

The teeth described here (BMNH 38646) are indistinguishable from those of typical rauisuchids such as *Rauisuchus* and *Prestosuchus* (Huene 1935–1942) (specimens in the Bayerische Staatssammlung für Paläontologie und historische Geologie, München). The maxilla is virtually identical in shape with that of other rauisuchians such as *Ticinosuchus* (Krebs 1965), *Saurosuchus* (Sill 1974), *Heptasuchus* (Dawley *et al.* 1979), and a new undescribed rauisuchid from SW Germany (R. Wild, pers. comm., specimens in Staatliches Museum für Naturkunde in Stuttgart, SMNS). This specimen shows two synapomorphies of the Rauisuchia: evidence of a movable joint between the maxilla and premaxilla, and a supplementary fenestra between maxilla and premaxilla (Benton 1984*a*) Within the Rauisuchia, *Teratosaurus* may be a rauisuchid (Bonaparte 1981; Galton 1985) or a poposaurid (Chatterjee 1985).

After 1861 many more fossil remains from the middle and late Triassic of Germany were assigned to *Teratosaurus*: teeth and skeletons (Huene 1908, 1915, 1932). Several authors (Colbert 1964; Walker 1964; Charig *et al.* 1965) have noted that the skeletons are very like those of prosauropod dinosaurs such as *Plateosaurus*, and they placed the Teratosauridae in the Prosauropoda (Palaeopoda: Colbert 1964) or left them as ‘Saurischia *incertae sedis*’ (Charig *et al.* 1965). However, there is no evidence for association of any of the skeletons with the teeth (Charig *et al.* 1965). It is likely that all ‘*Teratosaurus*’ skeletons belong to true prosauropods such as *Plateosaurus*, and that all *Teratosaurus* teeth belong to rauisuchids, or are indeterminate. *Teratosaurus* teeth are known from the Unterer and Mittlerer Stubensandstein of numerous localities in Baden-Württemberg (specimens in the Stuttgart and Tübingen collections). Teeth named as *Teratosaurus* have also been described from the middle Triassic of Germany (Fraas 1900) and England (Huxley 1870), but they cannot be identified to generic level.

### *Other Triassic ‘carnosaurs’*

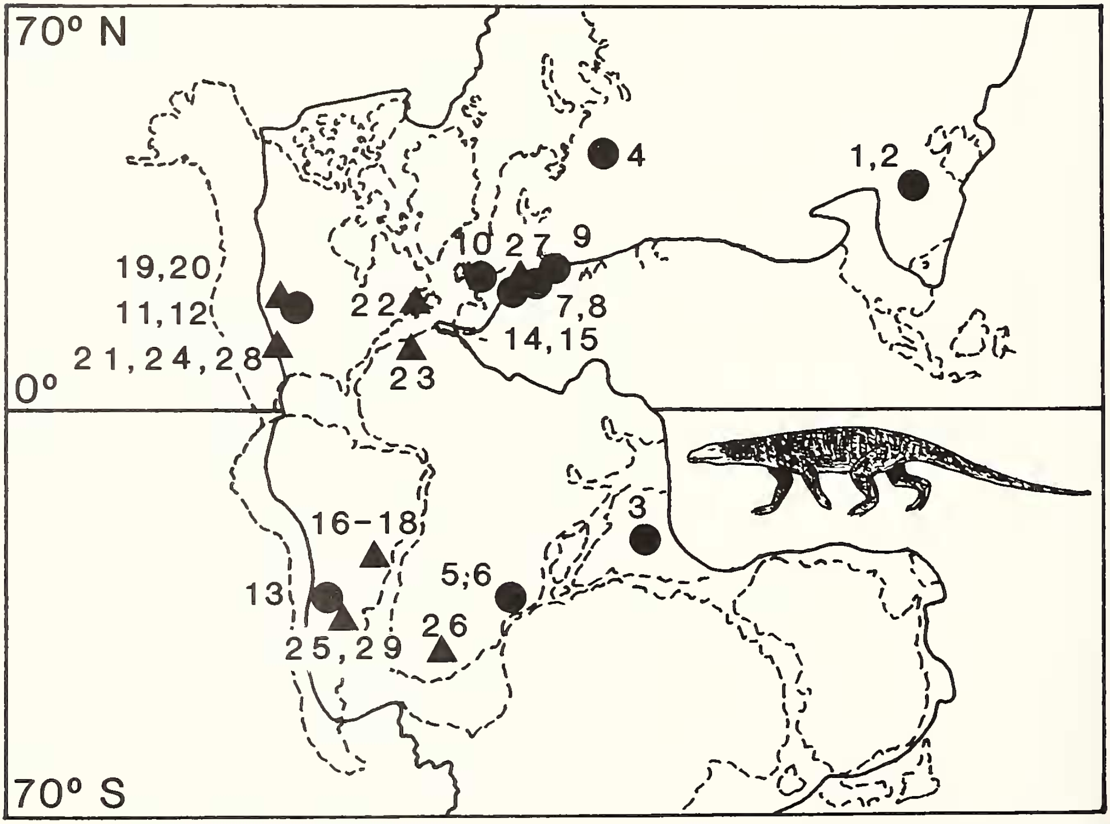
The genera other than *Teratosaurus* that have been called middle to late Triassic or early Jurassic carnosaurs include such forms as *Palaeosaurus* and *Cladeiodon* from England, *Palaeosaurus*, *Zanclodon*, and *Gresslyosaurus* from Germany, *Orosaurus*, *Aetonyx*, and *Gryponyx* from South Africa, *Zatomus* from North America, and *Sinosaurus* from China (Romer 1956). The type specimens of *Palaeosaurus* and *Cladeiodon* from England, and *Zatomus*, are teeth and, as such, they cannot be assigned with certainty to a particular group of dinosaurs or thecodontians: they are effectively indeterminate (Charig *et al.* 1965). *Palaeosaurus* from Germany is an anchisaurid prosauropod renamed *Efraasia* (Galton 1973). The type specimens of the several species of *Zanclodon* are teeth, again indeterminate. *Gresslyosaurus* is a large prosauropod dinosaur, and *Orosaurus* has been synonymized with the large prosauropod *Euskelosaurus* (Van Heerden 1979).

*Aetonyx* and *Gryponyx* are also prosauropod dinosaurs, probably identical to *Massospondylus* (Galton and Cluver 1976). *Sinosaurus* was based on a maxilla with teeth (dinosaur or thecodontian?) and postcranial remains very like those of a melanorosaurid prosauropod (Charig *et al.* 1965). This leaves no convincing evidence of large carnivorous dinosaurs in the Triassic.

### *Other doubtful early dinosaurs*

Many other remains of early 'dinosaurs' have been described from the middle and late Triassic of Germany in particular, and these have given the impression of a long early evolution of the group. In reviews of Triassic dinosaurs, Huene (1914*a*, 1932) noted the following earliest forms, listed here in stratigraphic order:

Lower Muschelkalk (Anisian): *Thecodontosaurus primus*, *Zanclodon silesiacus*, *Tanystropheus antiquus*, unnamed coelurosaur 'femora' (Huene 1914*b*).
Upper Muschelkalk (Ladinian): *Tanystropheus conspicuus*, *Procerosaurus cruralis*, *Teratosaurus schuetzii*, *Thecodontosaurus latespinatus*.
Lettenkeuper (Upper Ladinian): *Zanclodon laevis*, *Zanclodon crenatus*, *Avipes dillestedtianus*, and two 'typical coelurosaur teeth' (Huene 1932).
Schilfsandstein (Carnian): *Thecodontosaurus subcylindrodon*.



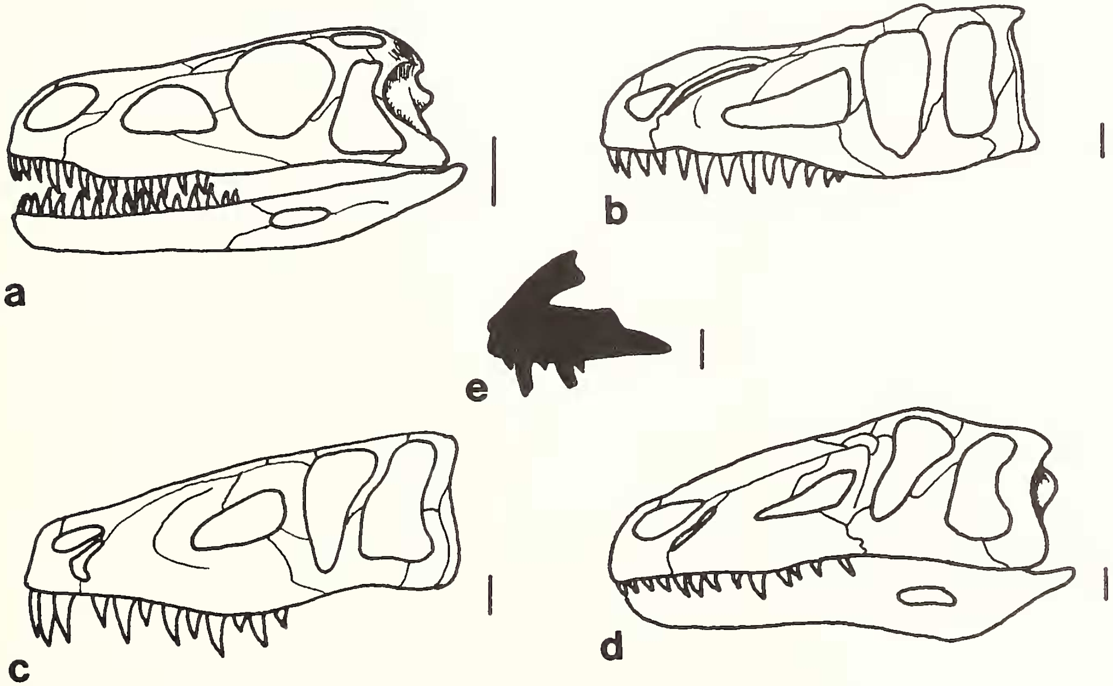
TEXT-FIG. 2. The distribution of rauisuchians plotted on a palaeogeographic map for the Triassic (Cox 1974). The modern continental outlines are shown with dashed lines, and the outlines of the Triassic supercontinent Pangaea are shown with a solid line. ● = Lower and Middle Triassic rauisuchians. ▲ = Upper Triassic rauisuchians. The numbers correspond to the twenty-nine genera of rauisuchians listed in Table 1.

Most of these species were based on single teeth or isolated damaged bones. Nevertheless, it now seems clear that none of these specimens is dinosaurian. Those named as *Tanystropheus*, *Procerosaurus*, *Thecodontosaurus latespinatus*, and *Z. laevis* belong to the prolacertiform *Tanystropheus* (Wild 1973). The other species of *Zanclodon*, *Thecodontosaurus*, and *Teratosaurus* noted above, as well as the 'coelurosaur teeth', are based on single teeth which could be prolacertiform or thecodontian. *Avipes* is based on a bundle of three incomplete 'metatarsals'. If that anatomical interpretation is correct, and this is not certain, they do not have any diagnostic characters of a dinosaur. The Lower Muschelkalk 'coelurosaur femora' (Huene 1914*b*) seem to be more like the distal ends of two humeri of a placodont such as *Cyamodus* (pers. obs.)!

### *The Rauisuchia*

The Rauisuchia includes several reptiles from the middle and late Triassic (Table 1; text-figs. 2, 3). These are characterized by the following features (Krebs 1976; Benton 1984*c*; Benton and Norman 1986):

1. Extra slit-like antorbital fenestra between premaxilla and maxilla.
2. Movable joint between maxilla and premaxilla.
3. Main antorbital fenestra is low in front.
4. Tall orbit with a 'stepped' postorbital/jugal bar behind.
5. Lacrimal forms a heavy 'eyebrow ridge' over the orbit.
6. Centra of dorsal vertebrae are very constricted in ventral view.
7. Reduced contact between pubis and ischium.



TEXT-FIG. 3. The skulls of some rauisuchids drawn to unit length. These are all reconstructions since no complete rauisuchid skull is known. The maxilla of *Teratosaurus* is shown (reversed) for comparison. *a*, *Ticinosuchus* (Krebs 1965); *b*, *Luperosuchus* (Romer 1971); *c*, *Heptasuchus* (Dawley *et al.* 1979); *d*, *Saurosuchus* (Sill 1974; Bonaparte 1981); *e*, *Teratosaurus*, BMNH 38646. The scale bars are 50 mm long. Note that *Ticinosuchus* (*a*) may have had the typical rauisuchid narrow fenestra between maxilla and premaxilla (Sill 1974).

TABLE 1. The genera of rauisuchians (Krebs 1976; Galton 1977; Bonaparte 1981, 1984; Chatterjee 1985) arranged in stratigraphic sequence (Oslen *et al.* 1982; Tucker and Benton 1982).

LOWER TRIASSIC

Scythian (Spathian)

1. ?*Wangisuchus*, Er-Ma-Ying Series, China.
2. ?*Fenhosuchus*, Er-Ma-Ying Series, China.

MIDDLE TRIASSIC

Anisian

3. '*rauisuchid*', Yerrapalli Formation, India.
4. *Vjushkovisaurus*, Donguz Series, Orenburg Region, USSR (Ochev 1982).
5. *Stagonosuchus*, Manda Formation, Tanzania.
6. '*Mandasuchus*', Manda Formation, Tanzania.

Anisian/Ladinian

7. *Ticinosuchus*, Grenzbitumenhorizont, Switzerland.
8. '*Ticinosuchus*', Grenzbitumenhorizont equivalent, Besano, North Italy (Pinna and Arduini 1978).
9. '*Ticinosuchus*', Fissure fillings, Gliny, Poland.

Ladinian

10. '*poposaurid*', Bromsgrove Sandstone Formation, England.
11. ?*Arizonasaurus*, Holbrook Member, Arizona, USA.
12. '*Anisodontosaurus*', Holbrook Member, Arizona, USA.
13. *Luperosuchus*, Chañares Formation Argentina.
14. '*Teratosaurus*', Lettenkeuper, South West Germany (Fraas 1900).
15. undescribed form, Lettenkeuper, South West Germany (Wild 1980).

UPPER TRIASSIC

Middle–Upper Carnian

16. *Rauisuchus*, Santa Maria Formation, Brazil.
17. *Prestosuchus*, Santa Maria Formation, Brazil.
18. ?*Procerosuchus*, Santa Maria Formation, Brazil.
19. *Poposaurus*, Popo Agie Formation, Wyoming, USA.
20. *Heptasuchus*, Popo Agie Formation, Wyoming, USA.
21. 'rauisuchid', Chinle Formation, Arizona, USA.
22. 'rauisuchid', Lower Wolfville Formation, Nova Scotia, Canada.
23. 'rauisuchid', Argana Formation, Argana, Morocco (Dutuit 1979).
24. unnamed forms, Dockum Formation, Texas, USA.
25. *Saurosuchus*, Ischigualasto Formation, Argentina.

Upper Carnian–Lower Norian(?)

26. 'rauisuchid', Lower Elliot Formation, South Africa (Galton 1985).

Middle Norian

27. *Teratosaurus*, Stubensandstein, South West Germany.
28. *Postosuchus*, (Upper) Dockum Formation, Texas, USA (Chatterjee 1985).

Upper Norian–'Rhaetian'

29. ?*Fasolasuchus*, Upper Los Colorados Formation, Argentina.

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8. Pubis attaches to an anteroventral facet on the ilium, rather than a ventral one.
9. Pubis has a distal 'foot' which is small in rauisuchids, but large in poposaurids.

The Rauisuchia contains two families, the Rauisuchidae and the Poposauridae which are distinguished from each other on the basis of characters of the skull and limbs (Chatterjee 1985). It is not possible at present to decide whether *Teratosaurus* was a rauisuchid or a poposaurid. Poposaurids may have been facultatively bipedal, and rauisuchids were large, 2–5 m long quadrupeds. They were powerful meat-eaters, and probably the top carnivores in their respective faunas. The Rauisuchia ranged in age from the latest Scythian to the Norian (latest early Triassic to late Triassic) (Table 1), and they radiated virtually world-wide during that time: rauisuchians are known from all continents except Australia and Antarctica (text-fig. 3). The Rauisuchia clearly fall within a group containing the phytosaurs, crocodiles, and aetosaurs—these all have the 'crocodile-normal' tarsus in which the astragalus forms a distal peg which fits into a deep socket on the calcaneum, and the two elements can rotate about his joint (Krebs 1976; Chatterjee 1982). Further, the Rauisuchia show close affinities with the Aetosauria, a late Triassic group of herbivorous archosaurs (Benton 1984*b*). All of these forms (termed the Pseudosuchia) share several synapomorphies in comparison with crocodiles and phytosaurs:

1. Frontal bone extends well forward and lies mainly in front of the orbits.
2. Iliac blade is oriented subhorizontally, rather than vertically.
3. Proximal distance between the ischia is less than that between the pubes.
4. Acetabulum is horizontal and faces downwards so that the femur fits directly into it. This gives all pseudosuchians a kind of erect gait that differs from the erect gait of dinosaurs, birds, and some early crocodile-like animals (Benton 1984*a*; Bonaparte 1984; Parrish 1984).

### *The Dinosauria*

The Pseudosuchia, including the rauisuchians, probably did not have any close relationship with the dinosaurs at all. The pseudosuchians and crocodiles form a completely separate evolutionary line from the dinosaurs, and their allies.

Until recently, and with only a few exceptions (e.g. Bakker and Galton 1974; Bonaparte 1976), the dinosaurs were thought to have evolved as several separate lineages that derived from ancestors in the middle Triassic, or earlier. However, a remarkable consensus of opinion has now been reached that the dinosaurs are a monophyletic group by several workers who have independently carried out cladistic analyses of the archosaurs (Benton 1984*c*; Norman 1984; Parrish 1984; Paul 1984; Sereno 1984; reviewed, Benton 1984*b*). The closest sister-groups of the Dinosauria are *Lagosuchus*, the Ornithosuchidae and, controversially, the Pterosauria (Padian 1984).

In conclusion, there is no evidence for an early radiation of large carnivorous dinosaurs in the Triassic. The 'Teratosauria' has been shown to be an unnatural assemblage of prosauropod skeletons, rauisuchian jaws, and unidentifiable teeth. The earliest dinosaurs were rare medium sized and small primitive forms and theropods from the late Triassic (middle-late Carnian) of the USA, Brazil, Argentina, Scotland, and India. A number of important reptile groups—rhynchosaurs, and many lineages of mammal-like reptiles and thecodontians—died out at the end of the Carnian (Benton 1986), and the theropods and prosauropods radiated subsequently in the Norian (Benton 1983). The rauisuchians, and other remaining thecodontians died out at the end of the Triassic, and the theropods and the prosauropods continued to radiate in the early Jurassic, together with the ornithopods. The first large carnivorous theropod dinosaurs ('carnosaurs'), appeared in the early and middle Jurassic.

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## NOTE ADDED IN PROOF

The Er-Ma-Ying Series of China (see Table 1) may in fact be Middle Triassic (Anisian) in age (Zhen *et al.* 1985). Welles (1984) describes *Teratosaurus suevicus* as 'a very large theropod, probably ancestral to megalosaurs, and is here included in the Megalosauridae', a view that is not accepted here.

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